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Effects of Delayed Mating on Reproductive Performance of *Ephestia cautella* [Walker] [Lepidoptera: Pyralidae]

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Abstract. The effect of age at mating of male and female warehouse moth, *Ephestia cautella* (Walker), soon after the emergence or delayed for 1-5 days was studied on the number of eggs laid (fecundity), egg viability, longevity and adult emergence. It was found that with the delay in mating after emergence of male, female or both, the number of eggs laid decreased proportionately. Egg viability decreased when female or both male and female were delayed from mating for more than 4 days. Male insects, that were delayed from mating, lived longer than the females delayed from mating. Average male and female longevity in all the treatments was 10 and 7 days, respectively. Delayed mating had significant effect on females than on males. Unmated males lived longer than the mated males. Thus methods that can delay and disrupt mating may be effective behavioural strategies for managing *E. cautella*.

Keywords: *Ephestia cautella*, mating delay, longevity, adult emergence, eggs

Introduction

The stored product moths are cosmopolitan, infesting a wide variety of harvest and food products such as cereals, dried fruits, cocoa beans, chocolates, candies and confectionery. They also infest dates, nuts, groundnuts and banana chips in storage. The stored product moths include tropical warehouse moth *Ephestia cautella* (Walker), rice moth *Corcyra cephalonica* (Stainton), Indianmeal moth *Plodia interpunctella* (Hubner), Angoumois grain moth *Sitoroga cerealella* (Olivioer) and *Euzopherodes vapidella* (Mann) (Akinneye *et al*., 2006). Infestation is mainly post-harvest. The moth feeds as larva, whereas all other stages are non-feeding. *Ephestia cautella* caused 60% weight loss and wheat seeds do not germinate after seven days of infestation. The infested product becomes unattractive for consumers due to production of silken thread, webbing the grains together; they also contaminate the stored products with feaces and other debris. The webbing also causes problems by forming clumps of grain that clog machinery during milling of grains to flour. *E. cautella* is a major pest of dried cocoa beans and its products, chocolates and cocoa powder in cocoa factory warehouse in Nigeria (Akinneye and Ashamo, 2006). The major control used against this pest is the use of conventional synthetic insecticides which are still the most effective means of controlling pests, despite their drawbacks including high mammalian toxicity and environmental pollution (Adedire and Ajayi, 1996). Mating is the major factor that determines the viability of eggs laid by any insect. In lepidopteran insect pests, delayed mating has detrimental effects on several life history traits including the number of eggs laid (fecundity), egg viability, pre-oviposition success and longevity (Jiao *et al*., 2006; Fangneng and Bhadriraju, 2003; Peralta *et al*., 1999; Knight, 1997; Spurgeon *et al*., 1997; Proshold, 1996; Walker, 1991; Unnithan and Payne, 1991; Wakamura, 1990; Lingren *et al*., 1988; Henneberry and Clayton, 1985; Ellis and Steele, 1982; Kehat and Gordon, 1977). Jiao *et al*. (2006) observed that 2 to 7 days delay in mating in *Chilo suppressalis* females lead to an 8-71% reduction in the number of viable eggs. Barrer (1976) reported that reproduction potential of *E. cautella* decreases with delayed age at mating resulting in decrease in the number of viable eggs. This was also observed in several species of moths such as *Heliothis virescens* and *Panolis flammea* (Proshold *et al*., 1982). Fangneng and Bhadriraju (2003) found that with delay in mating of *Plodia interpunctella* (Hubner), the number of eggs laid decreased. In the present study, we examined the effects of male and female age at mating on the period between adult emergence and egg laying (pre-oviposition), fecundity, egg viability and longevity. This information will be useful in developing mating disruption devices that can delay mating, thereby reducing the potential number of viable eggs, and thus the population of the insect.

Male and female adult moths, *E. cautella*, possess tympanic membranes on the lateral sides of the first abdominal segment (Mullen and Tsao, 1971) that respond to ultrasounds similar to those produced by insectivorous bats (Spangler, 1988). The tympanic membranes have evolved overtime to allow moths to avoid predation by insectivorous bats (Corner, 1999; Spangler, 1988) that emit ultrasonic pulses in the range

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of 20-200KHz (Fullard, 1998). Moths in flight show evasive manoeuvers when exposed to ultrasounds in that frequency range (Roeder, 1962; Treat, 1955). These manoeuvers include flying away from the sound or suddenly dropping to the ground and remaining motionless.

Materials and Methods

Insect culture. *Ephestia cautella* (Walker) was reared on the diet of cocoa powder in laboratory at 28±2 °C and 75±5% relative humidity. The diet (200 g) in two litre Kilner jars was infested with approximately 300 eggs. Corrugated paper spools, placed above the diet in each jar, served as pupation sites for wandering larvae. Sex of pupae collected from spools was determined using characters described by Butt and Cantu (1962). To ensure virginity, male and female pupae were placed in separate plastic containers measuring 13.5 cm in diameter and 12.5 cm deep. The plastic containers were checked twice daily and moths that emerged (0-12 h old) were used for the study.

Mating treatment. Newly emerging virgin females (0 day old) were paired with virgin males of six different ages: 0, 1, 2, 3, 4, or 5 days old (treatments 1-6). Newly emerging virgin males were paired with virgin females of five different ages: 1, 2, 3, 4, or 5 days old (treatments 7-11). Finally virgin females of five different ages (1, 2, 3, 4, or 5 days old) were mated with virgin males of the same age (treatments 12-16). For each of these 16 treatments, five females were paired with five males. As a control, five newly emerging virgin females were not paired with any male (treatment 17) and five newly emerged virgin males were not paired with any female (treatment 18). Each treatment was replicated six times making a total of 108 replicates (18 treatments with 6 replicates/treatment) and 540 adult male and 540 adult female moths (5 males and 5 females per replicate). Males and females were allowed to mate in glass vials (3 cm dia., 8 cm deep). After mating, vials were covered with mosquito netting (1.58 mm^2) and inverted over petri dishes for collection of the eggs dropping through the mosquito net. All the vials were kept in an insect breeding cage (70 cm ´ 60 cm ´ 50 cm). The number of eggs laid and the number of dead moths were counted daily between 8:00 am and 12:00 am. To estimate adult longevity, the jars were checked daily until all the adult moths died. The eggs were transferred to filter paper that was overlaid on moist cotton wool inside the closed petri dishes. Total number of eggs that hatched was recorded using a dissecting scope. Egg viability in each dish was calculated as the proportion of the total number of eggs that hatched. The life history traits measured were: pre-oviposition period, number of eggs laid, egg viability and male and female longevity.

Data analysis. A completely randomized design was used for the experiment (i.e. each treatment was randomized inside the insect breeding cages). Data on the pre-oviposition period, number of eggs laid, egg viability, adult (male and female) longevity were subjected to one-way ANOVA and where significant differences existed, means were separated using PROC GLM Procedure (SAS Institute, 1990). Linear regression (SAS Institute, 1990) was used to determine the relationship between mating delay (in days) and each of the life history traits was observed.

Results and Discussion

Effects of delayed mating on pre-oviposition period. Pre-oviposition period across all treatments was one day (i.e. the period between adult emergence and egg laying).

Effects of delayed mating on fecundity. Fecundity among treatments 1-17 was different, usually for an ANOV F = 3.198, $df_1 = 16$, $df_2 = 34$ and p = 0.002 (Table 1). More eggs were laid when there was no mating delay (treatment 1) than in any other treatment combination (Table 1). Virgin females laid about 27.0 non-viable eggs. In treatments where females, males or both sexes were delayed by 5 days, the number of eggs laid was not significantly different (P > 0.05). Fecundity decreased significantly (P = 0.000) as a function of male delay (Y = 270.067; d.f = 16; $r^2 = 0.904$ and F= 150.97), Female delay (Y = 239.489; d.f = 16; $r^2 = 0.853$, -47.890X; X = -47.890;

Table 1. Effect of delayed mating on facundity and egg viability of *E. cautella*

Male age (days)	Female age (days)	Mean number of eggs laid (MSD)	Mean number of viable eggs (MSD)
<24h	<24h	$235.33^{e} \pm 5.36$	$95.67^{d} \pm 4.93$
1	<24h	$163.00^{d} \pm 2.66$	$95.67^{d} \pm 4.93$
2	<24h	$148.33^{d} \pm 1.03$	$98.67^{d} \pm 0.57$
3	<24h	$76.33^{bc} \pm 0.74$	$61.33^{c} \pm 5.8$
4	<24h	$39.00^{abc} \pm 0.18$	$20.3^{b} \pm 4.20$
5	<24h	$18.00^{ab} \pm 1.00$	$0.00^{a} \pm 0.00$
<24h	1	$133.66^{d} \pm 4.64$	$96.00^{d} \pm 2.00$
<24h	2	$83.00^{c} \pm 5.73$	$90.00^{d} \pm 2.08$
<24h	3	$60.33^{bc} \pm 2.01$	$55.00^{c} \pm 7.22$
<24h	4	$27.00^{ab} \pm 3.71$	$29.67^{b} \pm 1.5$
<24h	5	$7.00^{a} \pm 0.08$	$0.00^{a} \pm 0.00$
1	1	$149.67^{d} \pm 8.7$	$96.00^{d} \pm 4.35$
2	2	$60.00^{bc} \pm 3.00$	$83.67^{d} \pm 5.5$
3	3	$43.00^{abc} \pm 2.00$	$58.67^{c} \pm 6.21$
4	4	$23.00^{ab} \pm 2.00$	$39.33^{b} \pm 9.01$
5	5	$15.66^{a} \pm 1.50$	$0.00^{a} \pm 0.00$
	Female only	$27..00^{e} \pm 8.2$	$0.00^{a} \pm 0.00$

Means followed by the same letters are not significantly different; P > 0.05 from each other using General Linear Model (GLM).

X = -42.410; = -42.410; P = 0.000 and F = 92.95), or both male and female delay (Y = 237.311; X = -42.724; d.f = 16; r^2 = 0.819, P = 0.000 and F = 72.46) (Tables 2, 3 and 4, respectively). Negative slopes of the regression equations indicate that fecundity decreased as males, females or both sexes were delayed from mating.

Effect of delayed mating on egg viability. Egg viability varied among treatments 1-17 (P = 0.000 and F = 4.4.447) and across the treatments ranged from 0.0% to 98.67% (Table 1). Egg viability among treatments, in which 0-3 days old males were mated with the newly emerging females, was not significantly different by a post-hoc test (P > 0.05) (Table 1).The number of viable eggs decreased when females or both sexes were delayed from mating for $\geq$ 4 days; for 5 days delay, the number of viable eggs was zero (Table 1). The decrease in the number of viable eggs as a function of moth age is greater in these treatments compared to the treatments when males or females only were delayed from mating. This indicates that egg viability was more strongly affected by both male and female age than by male or female age alone. There was a negative relationship between egg viability when both sexes were delayed (Y = 129.556; X = -9.23; -9.23X, d.f = 16 and r^2 = 0.864, P = 0.000 and F = 145.08) than when females were delayed (Y = 132.467; X = -20.37; -20.37X, d.f = 16 and r^2 = 0.864, P = 0.002 and F = 100.73) (Tables 2 and 3). However, there was no relationship between egg viability and male delay (Table 4).

Table 2. Regression analysis with female delay as a function of other factors

Department	r^2	d. f	F-Statistics	P-value	Y	X
Male longevity	0.015	16	0.25	0.626	11.7333	0.0762
Female longevity	0.400	16	10.65	0.005	5.9778	0.3238
Adult emergence	0.868	16	105.64	0.000	132.822	-21.314
Eggs laid/ fecundity	0.853	16	92.95	0.000	239.489	-42.410
Egg viability	-0.864	16	101.30	0.000	132.467	-20.371

Table 3. Regression analysis with both male and female delay as a function of other factors

Department	r^2	d. f	F-Statistics	P-value	Y	X
Male longevity	0.183	16	3.58	0.077	9.9111	0.3429
Female longevity	0.310	16	7.18	0.016	5.4444	0.2381
Adult emergence	0.906	16	155.07	0.000	126.333	-19.7620
Eggs laid/ fecundity	0.819	16	72.460	0.000	237.311	-42.724
Egg viability	0.864	16	101.44	0.000	129.556	-19.238

Effects of delayed mating on adult longevity. Effects of delayed mating on adult longevity of females ranged from 5.33±0.12 to 9.33±0.40 days and male longevity from 9.33±0.02 to 14.33±0.61 days (Table 5). A comparison among treatments showed that delay in mating of females had significant effect than that of males (Tables 2 and 4, respectively). Average longevity of males and females in all the treatments was 7.33±0.31 and 12.33±0.02, respectively (Table 5). The longevity of virgin males and females was 13.67±0.42 and 7.67±0.30, respectively (Table 5). The longevity of virgin males was significantly (P<0.05) higher than that of virgin females. Linear regressions indicated a positive relationship (P = 0.003) between male longevity (Y) and male delay (Y = 11.755; X = 0.419; + 0.419×; d.f = 16; r^2 = 0.660, F=12.40) and also between female longevity (Y) and female delay (Table 2). It appears that the slope of the female delay regression (0.323) is steeper than that of the male delay regression (0.419) indicating that mating delay increases the male longevity more than the female longevity. Linear regression also indicated positive relationship when both males and females were delayed (Table 3).

Effects of delayed mating on adult emergence. Males delayed for less than 24 hs to 5 days had adult emergence ranging from 87 to 97%, females delayed for 1-4 days had adult

Table 4. Regression analysis with male delay as a function of other factors

Department	r^2	d. f	F-Statistics	P-value	Y	X
Male longevity	0.437	16	12.40	0.003	11.7556	0.4190
Female longevity	0.770	16	53.65	0.000	5.6222	0.6952
Adult emergence	0.497	16	15.84	0.001	127.111	-14.333
Eggs laid/ fecundity	0.904	16	150.97	0.000	270.067	-47.590
Egg viability	0.458	16	13.52	0.002	128.422	-14.105

emergence ranging from 13 to 92% while males and females delayed for 1-4 days had adult emergence ranging from 20 to 91% (Table 6). Female delay had significant effect by reducing adult emergence than male delay. Increasing the female delay and both male and female delay significantly decreased adult emergence than the male delay by post-hoc test.

Table 5. Effect of delayed mating on longevity of adult *E. cautella* (Walker)

Male age (days)	Female age (days)	Male longevity (days) (M±SD)	Female longevity (days) (M±SD)
<24h	<24h	$12.00^{cd} \pm 0.00$	$6.33^{abc} \pm 0.21$
1	<24h	$12.33^{de} \pm 0.02$	$6.67^{bcd} \pm 0.24$
2	<24h	$13.33^{df} \pm 0.40$	$7.67^{de} \pm 0.30$
3	<24h	$13.67^{ef} \pm 0.42$	$9.00f^{g} \pm 0.38$
4	<24h	$14.33^{f} \pm 0.61$	$9.33^{g} \pm 0.40$
5	<24h	$13.67^{ef} \pm 0.42$	$9.33^{g} \pm 0.40$
<24h	1	$11.67^{bc} \pm 0.00$	$6.67^{bcd} \pm 0.24$
<24h	2	$11.67^{bc} \pm 0.00$	$6.67^{bcd} \pm 0.24$
<24h	3	$12.33^{de} \pm 0.02$	$7.33^{cde} \pm 0.31$
<24h	4	$13.67^{ef} \pm 0.42$	$8.00^{ef} \pm 0.00$
<24h	5	$11.00^{bc} \pm 0.00$	$7.67^{de} \pm 0.30$
1	1	$9.33^{a} \pm 0.02$	$5.67^{a} \pm 0.11$
2	2	$9.66^{a} \pm 0.04$	$5.33^{a} \pm 0.12$
3	3	$11.00^{bc} \pm 0.00$	$6.33^{abc} \pm 0.21$
4	4	$12.33^{de} \pm 0.35$	$7.00^{cde} \pm 0.00$
5	5	$12.33^{de} \pm 0.35$	$7.00^{cde} \pm 0.00$
	Male only	$13.67^{ef} \pm 0.42$	
	Female only		$7.67^{de} \pm 0.30$

Mean followed by the same letter are not significantly different; P > 0.05 from each other using General Linear Model (GLM).

Table 6. Effect of delayed mating on emergence of adult *E. cautella*

Male age (days)	Female age (days)	Adult emergence (%) (M±SD)
<24h	<24h	$95.67^{e} \pm 4.93$
1	<24h	$93.00^{e} \pm 5.19$
2	<24h	$97.00^{e} \pm 2.64$
3	<24h	$87.67^{d} \pm 4.04$
4	<24h	$88.33^{de} \pm 1.52$
5	<24h	$0.00^{a} \pm 0.00$
<24h	1	$92.67^{e} \pm 3.05$
<24h	2	$89.00^{de} \pm 2.64$
<24h	3	$58.33^{c} \pm 17.15$
<24h	4	$13.67^{ab} \pm 5.50$
<24h	5	$0.00^{a} \pm 0.00$
1	1	$91.00^{e} \pm 1.00$
2	2	$75.00^{d} \pm 4.50$
3	3	$54.67^{c} \pm 2.5$
4	4	$26.67^{b} \pm 5.77$
5	5	$50.00^{a} \pm 0.05$

Mean followed by the same letters are not significantly different; P > 0.05 from each other using General Linear Model (GLM).

The pre-oviposition periods observed in this study were not affected when males were delayed from mating for 24 h to 5 days. There were no significant difference (P > 0.05) when males were delayed from mating for less than 24 hs to 5 days (Table 1). The pre-oviposition periods, when males were delayed for 24 h to 5 days, were similar to those observed for unmated females (Treatment 18). The pre-oviposition period of the spiny bollworm, *Earias insulana* (Boisduval) also, was significantly prolonged in unmated females, enabling the females to delay oviposition until after mating (Kehat and Gordon, 1977). It means that mating promotes pre-oviposition in *E. insulana* (Boisduval). Pre-oviposition period increased when females were delayed from mating (Kehat and Fiordon, 1977). Similarly, Jiao *et al.* (2006) found that the pre-oviposition period was delayed or prevented in *E. insulana* (Boisduval). *E. cautella* fecundity was the highest when there was no mating delay (Table 1). This finding was in agreement with the findings of Fangneng and Bhadriraju (2003) that *Plodia interpunctella* fecundity was the highest when there was no mating delay. In this study, the fecundity of females older than or equal to 4 days reduced significantly. The reproductive potential of the females decreased with delayed age at mating. This result coincides with the work of Barrer (1976) that reproductive potential of *E. cautella* decreases with increase in age at mating; this was also observed in several species of moths such as in *Heliothis virescens*, *Penolis flammea* (Leather *et al*., 1985; Proshold *et al*., 1982) *Chilo partellus* (Unnithan and Payne, 1991) and *Lobesia botrana* (Torres-vila *et al*., 2002). The result obtained in the present study showed that egg viability was affected by age of both males and females by post-hoc test. When males were 4 days old, 20% of the eggs laid by the females were viable. Delayed mating of males and females had significant effect on egg viability, producing 20% viable eggs at 4 days. Five days old males failed to inseminate the females. Consequently, sperms were unavailable to fertilize the eggs or perhaps the sperms had degenerated. The eggs laid by females when males were 5 day old were similar to those laid by virgin females, and in both the cases, the eggs failed to hatch (Table1). Mating and transfer of sperms is important for egg maturation and egg viability (Park *et al*., 1998; Ramaswamy *et al*., 1997; Henneberry and Clayton, 1985). Jiao *et al*. (2006) observed that 2-7 days delay in mating in *C. suppressalis* females lead to an 8-71% reduction in the potential number of viable eggs. This observation was also similar to that of Fangneng and Bhadriraju (2003) that viability of *Plodia interpunctella* eggs decreased concurrent with the delay in female mating. The decrease in egg viability with female age may be due to eggs not being fertilized (Fangneng and Bhadriraju, 2003). The number of degenerating oocyte-release in unmated females increases with age, and this could have prevented spermatophores from reaching the bursa copulatrix when females were eventually mated with males (Lum, 1983; 1982). Reduction in viable eggs with delayed mating is likely to result from deterioration in egg viability with time and oocyte degeneration interfering with sperm migration and successful egg fertilization. The present results indicated that the earlier a female mated, the shorter was its longevity, a correlation reported for many other Lepidopterous species (Lingren *et al*., 1988; Ellis and Steele, 1982; Proshold *et al*., 1982). Increased longevity with delay of mating is widely considered to be a result of reduced energy consumption associated with reproduction. Although data were not collected, some of the eggs that failed to hatch in these experiments were not embryonated. Lum and Flaherty (1969) reported that mated *P. interpunctella* moths lived for approximately 5-7 days; this was still within what was observed in the case of *E. cautella*. Linear relationships observed between longevity of either male or female and corresponding delay in male, female or both male and female mating may have been confounded with the days the moths were delayed. For instance, in the treatment of 5 days delay treatment, it was impossible for moths to have lived to < 5 day. From the practical standpoint, mating delay did not have a greater impact on adult longevity. Similar results between delayed mating and longevity were observed with *L. dispar*, but not with shoot stem borer, *Chilo partellus* (swindhoe) (Unnithan and Payne, 1991). Increased female longevity associated with mating delay has been reported in several other species of Lepidoptera (Lingren *et al*., 1988; Henneberry and Clayton, 1985; Ellis and Steele, 1982; Proshold *et al*., 1982). Female delay had significant effect on adult emergence then the male delay.

In conclusion, the number of eggs laid and egg viability were significantly reduced when adult male, female or both male and female *E. cautella* were delayed from mating. Delaying females than the males from mating had a greater impact on egg laying. This result suggests that techniques such as the use of high pheromone concentrations, which can aggregate more females than males, will reduce the chances of mating (Jones, 1988a; 1988b) or by production of ultrasound, similar to those produced by insectivorous bats, the moth may invest more energy into evasive manoeuvers and less into finding mates. (Mullen and Tsao, 1971). Trematerra and Pavan (1995) suggested that the use of the technology of mating-delay may be a promising non-chemical pest management method for *E. cautella* for two reasons. First, *E. cautella* males and females do not feed as adults and live for 6-14 days after emergence; their sole purpose is to mate and lay eggs. Secondly, during the short adult life, if moths are exposed to ultrasound they may invest more energy into evasive manoeuvers and less in finding mates and courtship behaviour; by reducing the chances of successful mating, population may be reduced to a level where they do not cause economic damage to stored products.

References

Adedire, C.O., Ajayi, T.S. 1996. Assessment of the insecticidal properties of some plant extracts as grain protectants against maize weevil, *Sitophilus zeamais* (Motschulsky). *Nigerian Journal of Entomology* **13:** 93-101.

Akinneye, J.O., Adedire, C.O., Arannilewa, S.T. 2006. Potential of *Cleisthopholis patens* Elliot as maize protectant against the stored product moth *Plodia interpunctella* (Hubner) (Lepidoptera: Pyralidae). *African Journal of Biotechnology* **25:** 2515-2525.

Akinneye, J.O., Ashamo, M.O. 2006. Some aspects of the biology of the yam moth, *Euzopherodes vapidella* Mann (Lepidoptera; Pyralidae), a pest of stored yam tuber in Nigeria. *Journal of Entomological Research* **30:** 59-63.

Barrer, P.M. 1976. The influence of delayed mating on the reproduction of *Ephestia cautella* (Walker) (Lepidoptera; Pyralidae). *Journal of Stored Product Research* **12:** 165-169.

Butt, B.A., Cantu, E. 1962. *Sex Determination of Lepidopterous Pupae*. USDA Agricultural Research Service Report, 7 pp., United States Department of Agriculture.

Corner, W.E. 1999. Un chant d'appel amoureux. Acoustic communication in moths. *Journal of Experimental Biology* **202:** 1711-1723.

Ellis, P.E., Steele, G. 1982. Effects of delayed mating on fecundity of females of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae). *Bulletin of Entomological Research* **72:** 295-302.

Fangneng, H., Bhadriraju, S. 2003. Effects of delayed mating on reproductive performance of *Plodia interpunctella* (Hubner) (Lepidoptera: Pyralidae). *Journal of Stored Product Research* **39:** 53-63.

Fullard, J.H. 1998. Sensory coevolution of moths and bats. In: *Comparative Hearing Insects*, R. R. Hay, A. N. Popper and R. R. Fay (eds.), Springer, New York, USA.

Henneberry, T.J., Clayton, T.T. 1984. Time of emergence, mating, sperm movement and transfer of ejaculatory duct secretory fluid by *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) under reversed light-dark cycle laboratory conditions. *Annals of the Entomological Society of America* **77:** 301-305.

Henneberry, T.J., Clayton, T.E. 1985. Tobacco budworm moths (Lepidoptera: Noctuidae): Effect of time of emergence, male age and frequency of mating on sperm transfer and egg viability. *Journal of Economic Entomology* **78:** 379-382.

Jiao, X., Xuam, W., Sheng, C. 2006. Effects of delayed mating and male mating history on longevity and reproductive performance of rice stem borer, *Chilo suppressalis*

(Walker) (Lepidoptera, Pyralidae). *Journal of Applied Entomology* **130:** 108-112.

Jones, O.T. 1988a. Practical applications of pheromones and other semiochemicals. In: *Insect Pheromones and Their Use in Pest Management*, P. Howse, I. Stevens and O. Jones (eds.), pp. 263-352, Chapman & Hall, London, UK.

Jones, O.T. 1988b. The commercial exploitation of pheromones and other semiochemicals. *Pesticide Science* **54:** 293-296.

Kehat, M., Gordon, D. 1977. Mating ability, longevity and fecundity of the spiny bollworm, *Earias insulana*, (Lepidoptera; Noctuidae). *Entomologia Experimentalis et Applicata* **22:** 688-698.

Knight, A.L. 1997. Delay of mating of codling moth in pheromone disrupted orchards. *Technology Transfer in Mating Disruption IOBC Bulletin* **20:** 203-206.

Leather, S.R., Watt, A.D., Barbour, D.A. 1985. The effect of host plant and delayed mating on the fecundity and life span of the pine beauty moth, *Panolis flammea*: their possible influence on population dynamics and relevance to pest management strategies. *Bulletin of Entomological Research* **75:** 641-651.

Lingren, P.O., Warner, W.B., Henneberry, T.J. 1988. Influence of delayed mating on egg production, egg viability, mating and longevity of female pink bollworm (Lepidoptera: Gelechiidae). *Environmental Entomology* **17:** 86-89.

Lum, P.T.M. 1982. Degenerating oocytes: a physical barrier to sperm translocation in female *Plodia interpunctella* (Hubner) and *Ephestia cautella* (Walker). *Journal of Georgia Entomological Society* **17:** 421-428.

Lum, P.T.M. 1983. Oocyte degeneration in *Plodia interpunctella* Hubner and *Cadra cautella* (Walker) (Lepidoptera: Pyralidae): Influence of temperature and humidity. *Environmental Entomology* **12:** 1539-1541.

Lum, P.T.M., Flaherty, B.R. 1969. Effect of mating with males reared in continuous light or in light-dark cycles on fecundity in *Plodia interpunctella* (Hubner) (Lepidoptera: Phralidae). *Journal of Stored Product Insect Research* **5:** 89-94.

Mullen, M.A., Tsao, C.H. 1971. Tympanic organ of Indian meal moth, *Plodia interpunctella* (Hubner), almond moth, *Cadra cautella* (Walker) and tobacco moth, *Ephestia calutella* (Hubner). (Lipidoptera: Pyralidae). *International. Journal of Insect Morphology and Embryology* **1:** 3-10.

Park, Y.I., Ramaswamy, S.B., Srinivasan, A. 1998. Spermatophore formation and regulation of egg maturation and oviposition in female *Heliothis virescens by* the male. *Journal of Insect Physiology* **44:** 903-908.

Peralta, V., Cuesta, M.J., Mata, I., Serrano, J.F., Perez-Nievas, F., Natividad, M.C., Fadamiro, H.Y., Baker, T.K. 1999. Reproductive performance and longevity of female European corn borer, *Ostrinia nubilalis*: effect of multiple mating, delay in mating and adult feeding. *Journal of Insect Physiology* **45:** 385-392.

Proshold, F.I. 1996. Reproductive capacity of laboratory-reared gypsy moths (Lepidoptera: Lymantriidae): effect of age of female at time of mating. *Journal of Economic Entomology* **89:** 337-342.

Proshold, F.I., Karpenko, C.P., Graham, C.K. 1982. Egg production and oviposition in the tobacco budworm: effect of age at mating. *Annals of the Entomological Society of America* **75:** 51-55.

Ramaswamy, S.B., Shu, S., Park, Y.I., Zeng, F. 1997. Dynamics of juvenile hormone-mediated gonadotropism in the Lepidoptera. *Archives of Insect Biochemistry and Physiology* **35:** 539-558.

Roeder, K.D. 1962. The behaviour of free-flying moths in the presence of artificial ultrasonic pulses. *Animal Behaviour* **10:** 300-304.

SAS Institute Inc. 1990. *SAS/STAT User's Guide*, Version 6, 4th edition, SAS Institute, Cary, NC, USA.

Spangler, H.G. 1988. Moth hearing, defense and communication. *Annual Review of Entomology* **33:** 59-81.

Spurgeon, D.W., Raulston, J.R., Lingren, P.D., Shaver, T.N. 1997. Mexican rice borer (Lepidoptera: Pyralidae) reproductive responses to delayed mating. *Southwestern Entomologist* **22:** 195-200.

Torres-Vila, L.M., Rodriguez-Molina, M.C., Stockel, J. 2002. Delayed mating reduces reproductive output of female European grapevine moth, *Lobesia botrana* (Lepidoptera; Tortricidae). *Bulletin of Entomological Research* **92:** 241-249.

Treat, A.E. 1955. The response to sound of certain Lepidoptera. *Annals of the Entomological Society of America* **48:** 272-284.

Trematerra, P., Pavan, G. 1995. Ultrasound production in the courtship behaviour of *Ephestia cautella* (Walker), *E. kuehniella Z.* and *Plodia interpunctella* (Hb) (Lepidoptera; Pyralidae). *Journal of Stored Product Research* **31:** 43-48.

Unnithan, G.C., Payne, S.O. 1991. Mating, longevity, fecundity, and egg fertility of *Chilo partellus* (Lepidoptera: Pyralidae): effects of delayed or successive mating and their relevance to pheromonal control methods. *Environmental Entomology* **20:** 150-155.

Wakamura, S. 1990. Reproduction of the beet armyworm, *Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae), and influence of delayed mating. *Japanese Journal of Applied Entomology and Zoology* **34:** 43-48.

Walker, P.W. 1991. Effects of delayed mating on the reproduction of *Pectinophora scutigera* (Holdaway) (Lepidoptera: Gelechiidae). *Journal of the Australian Entomological Society* **30:** 339-340.